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Heartfelt embodiment: Changes in body-ownership and self-identification produce distinct changes in interoceptive accuracy

Maria L. Filippetti *, Manos Tsakiris

Royal Holloway, University of London, Department of Psychology, Egham, TW20 0EX Surrey, UK

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ABSTRACT

Interoceptive and exteroceptive information are both essential for the construction and update of self-awareness. Whereas several studies have shown how interoceptive accuracy or cardiac feedback influences body-awareness, no studies have looked at the reverse effect, namely how exteroceptively-driven changes in body-ownership and self-identification can influence individuals' ability to detect internal bodily signals. We exposed participants to the Rubber Hand Illusion (Experiment 1) and to the Enfacement Illusion (Experiment 2), and tested how this change in the sense of body-ownership and self-identification affected their interoceptive accuracy (IAcc). The heartbeat-counting task was used to measure IAcc before the bodily illusions, and then the same task was interleaved with periods of visuo-tactile stimulation, during which synchronous and asynchronous multisensory stimulation was applied. We found that a change in body-ownership significantly improved performance of participants with lower interoceptive accuracy. In contrast, a change in self-identification significantly decreased performance of participants with higher interoceptive accuracy. These results suggest that changes in different domains of self-awareness can differentially impact individuals' ability to accurately detect signals arising from within the body, highlighting the distinct role that interoceptive signals play for different facets of bodily self-consciousness.

1. Introduction

Bodily self-consciousness (BSC) results from the integration of two fundamental sources of body-related information, namely signals arising from the body as perceived from the *outside* and external environment (i.e. exteroception) and from *within* the body (i.e. interoception). The perception of the body from the *outside* has been shown to be essential in order to maintain and update BSC. For example, the integration of multisensory signals has been shown to play a fundamental role in body-ownership (Botvinick & Cohen, 1998; Ehrsson, 2007; Lenggenhager, Tadi, Metzinger, & Blanke, 2007; Tsakiris, 2010) and self-identification (Tsakiris, 2008). Bodily illusions such as the Rubber Hand Illusion (RHI) can modulate the awareness of one's own body through the manipulation of visual and tactile synchrony (Botvinick & Cohen, 1998). In these experiments, seeing a rubber hand being stroked together with one's own hidden hand provokes a change in body-ownership, whereby the rubber hand is perceived as belonging to one's own body (Botvinick & Cohen, 1998; Tsakiris & Haggard, 2005). The influence of multisensory integration in updating our sense of body awareness has been shown in several other contexts, such as full body illusions (e.g. Ehrsson, 2007; Lenggenhager et al., 2007) and self-identification (i.e. see the Enfacement Illusion (EI), Tsakiris, 2008). In the Enfacement Illusion, synchronous interpersonal multisensory stimulation (IMS) between the participant's face and another person's face evokes a measurable change in self-recognition, whereby a certain percentage of the other person's face is identified as "self" (Tajadura-Jiménez, Longo, Coleman, & Tsakiris, 2012), indicative of altered self-other boundaries (Cardini, Tajadura-Jiménez, Serino, & Tsakiris, 2013; Paladino, Mazzurega, Pavani, & Schubert, 2010; Tajadura-Jiménez & Tsakiris, 2014). Together, these findings seem to suggest that similar exteroceptive sensory processes are involved at different levels of body-awareness, from the ability to define ownership towards a body-part, to the ability to identify with one's own face.

Exteroceptive signals however are not the only relevant sources of information about the self. Together with exteroception, internal signals arising from within the body are essential in order to maintain a sense of self (Tsakiris, Tajadura-Jiménez, & Costantini, 2011).

* Corresponding author at: University College London, Department of Clinical, Educational and Health Psychology, 1-19 Torrington Place, WC1E 7HB London, UK.
E-mail addresses: m.filippetti@ucl.ac.uk (M.L. Filippetti), manos.tsakiris@rhul.ac.uk (M. Tsakiris).

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Interoceptive awareness – that is often operationalized as Interoceptive Accuracy (IAcc) – is the ability to perceive internal bodily signals such as cardiac activity, hunger, and distension of bladder and other visceral organs (Craig, 2002, 2010). IAcc has been considered a rather stable trait, whereby some individuals seem to be better than others in detecting and becoming aware of internal bodily signals (Herbert & Pollatos, 2012). Nevertheless, a renewed interest in the topic of interoception has provided preliminary evidence of the interactive relationship between interoceptive and exteroceptive bodily signals.

Direct behavioural evidence of the effects of interoception on body-ownership comes from three recent studies. The first study that tested the potential link between exteroceptive and interoceptive awareness of the body measured and quantified IAcc and compared this measure with the change in body-ownership caused by multisensory stimulation, using the RHI as a paradigmatic case of the exteroceptive self. Tsakiris et al. (2011) observed a negative correlation between IAcc and RHI, such that people with lower IAcc showed a stronger RHI measured behaviourally and homeostatically (i.e. drop in skin temperature), suggesting that, in the absence of accurate interoceptive representations, one's model of self is predominantly exteroceptive. Following this finding, two studies used cardio-visual feedback synchronous with one's own heartbeat to induce changes in body-ownership (Aspell et al., 2013; Suzuki, Garfinkel, Critchley, & Seth, 2013). Aspell et al. (2013) used cardio-visual illumination of a virtual body either in synchrony or asynchrony with respect to the participant's heartbeat to show changes in body-ownership, providing evidence of the integration between internal and external signals of the body. On a similar line of research, Suzuki et al. (2013) demonstrated the influence of interoceptive signals at the exteroceptive level by applying cardio-visual feedback to implement the RHI. In their study, participants were exposed to a virtual RHI set-up and experienced an increased illusion during synchronous cardio-visual feedback, compared to asynchronous feedback (Suzuki et al., 2013). More recently, studies have focused on the effect of pleasant affective touch, which is known to engage interoceptive processing, on body-ownership (Crucianelli, Metcalf, Fotopoulou, & Jenkinson, 2013; Lloyd, Gillis, Lewis, & Farrell, 2013; van Stralen et al., 2014), suggesting again the influence of interoceptive cues on external signals related to the body. Taken together, these findings suggest that the relation between the perception of the body from the outside (i.e. exteroception) and the perception of the body from the inside (i.e. interoception) is fundamental to the coherence of the bodily self: their integration enables the self to feel grounded in a coherent body that consists of both exteroceptive and interoceptive representations. However, while these studies focused on the role of interoceptive signalling or levels of IAcc in modulating the experience of the body as perceived from the outside, the question of whether exteroceptively-driven changes in body-awareness can in turn influence interoceptive awareness remains unanswered.

A recent unifying account of the self proposes that self-related information results from the integration between incoming sensory events with the existent mental representation of the self (Apps & Tsakiris, 2014; Limanowski & Blankenburg, 2013). According to this predictive coding model of the self (Seth, Suzuki, & Critchley, 2011), incoming sensory inputs are interpreted in light of prediction signals derived from existing priors about the self (Apps & Tsakiris, 2014). The system's ultimate goal is to reduce 'free energy', by minimising prediction errors through a process of matching between incoming information and its predictions (Apps & Tsakiris, 2014; Limanowski & Blankenburg, 2013; see also for Samad, Chung, & Shams, 2015 for direct evidence). In the context of maintaining an integrated sense of self, any update of self-representations is dependent upon prior beliefs derived from past events, with the aim of minimising prediction errors in favour of the most likely 'self' (Apps & Tsakiris, 2014). Thus, body-related multisensory signals (such as those implemented during the RHI and EI) may explain away prediction errors by creating a new model of the self, that incorporates the fake rubber hand or the other face into the self-mental representation (Suzuki et al., 2013). This change in BSC will result in an update of posterior probabilities and a decrease in the probability that one's actual body or face is represented as 'self' (Apps & Tsakiris, 2014). As a result, one could expect an increase in top-down attention to the self, which in turn will produce an enhanced general precision of all self-relevant data, including interoceptive inputs. Previous studies have addressed the role of interoceptive signals in the multisensory predictive model of the self (Aspell et al., 2013; Suzuki et al., 2013). This investigation aimed to test the opposite effect, namely the influence of exteroceptive signalling in modulating the experience of the body from within.

In line with recent accounts, we assume that the self is a multilevel, multimodal construct, continually updated in the brain from all available interacting cues including interoception (Apps & Tsakiris, 2013; Seth, 2013). Precision necessarily varies along this hierarchy (Edwards, Adams, Brown, Pareés, & Friston, 2012). Self-focus can therefore enhance the precision of all self-relevant and self-specifying signals, including interoceptive prediction errors, thus enabling updating of priors in interoceptive systems and consequent perception of heartbeats. If self-focus enhances the precision of a high-level (conscious) prior for the multimodal self, this will affect the precision of priors and prediction errors at lower levels of the self-hierarchy (including those for the heartbeat itself). How such self-focus affects interoception under conditions that induce a change in self-representations induced by bodily illusions remains unknown. In the present study, we tackle two issues. First, we explore whether changes in body-awareness after exposure to the RHI and EI can affect individuals' accuracy in detecting their internal bodily signals, quantified by the heartbeat-counting task (Schandry, 1981). To answer this question, we conducted two experiments using two different bodily illusions in two independent samples of participants. In Experiment 1, we manipulated the experience of body-ownership through the use of the RHI to measure changes in IAcc, whereas in Experiment 2 we used the Enfacement Illusion to test whether changes in self-identification will lead to changes IAcc. Second, we were interested to test whether the hypothesised modulations of IAcc would be comparable across the two illusions. Even though recent findings on the relationship between changes in body-ownership and IAcc and changes in self-identification and IAcc (Tajadura-Jiménez, Grehl, & Tsakiris, 2012; Tajadura-Jiménez, Longo, et al., 2012; Tsakiris et al., 2011) have shown consistent results, namely that lower levels of IAcc were correlated with stronger illusions, the question of how changes in body- versus self-face representations elicited by the RHI and EI respectively can affect processing in the interoceptive domain remains unanswered. This question is important because of the distinctive role that one's face plays not only for body-awareness but also for the representation of one's identity in relation to others. Nothing provides such a strong sense of self as looking at one's own face, and the enfacement illusion, as an experimental model of self-identification has been shown to alter self-other boundaries (Cardini et al., 2013; Paladino et al., 2010; Tajadura-Jiménez & Tsakiris, 2014). We therefore hypothesised that the experience of the RHI and EI would modulate performance in the heartbeat task differently. In particular, we hypothesised that individuals with lower-IAcc at baseline would show a significant increase in their IAcc after exposure to the RHI, where body-ownership is manipulated, consistent with past findings on the effects of self-processing on IAcc (Ainley, Tajadura-Jiménez, Fotopoulou, & Tsakiris, 2012). Specifically, we hypothesised that in these individuals exposure to the bodily illusion would increase